Nerilla an Archiannelid.

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With Plates 38–41.

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Introduction.

The little worm which forms the subject of this paper was found by me in the month of May of last year, 1911, in one of the sea-water tanks of the Stazione Zoologica at Naples.[1] On close inspection it turned out to be a member of that

[1] I wish here to express my thanks to the authorities of Cambridge University, who granted me the use of a table at Naples.

somewhat ill-defined group known as the Archiannelida. Under the impression that it was quite a new form, I was on the point of issuing this account of its habits and structure when I discovered that M. de Beauchamp had last year begun to publish a description of this very animal in the 'Bull. Scient. de la France et de la Belgique' (**2**).[1] It appears to be no other than the Nerilla antennata, so named by O. Schmidt in 1848 (**21**), and hitherto considered as an aberrant Polychæte. Since then de Quatrefages (**16**) and Claparède (**3**) have written about it, and Miss Pereyaslawzewa (**13**) published a long account of its anatomy, which (as already pointed out by de Beauchamp) is neither complete nor correct. To M. de Beauchamp belongs the credit of having begun the first accurate account of Nerilla, and of having first pointed out its resemblances to Protodrilus.

General Appearance and Habits.

Nerilla antennata is a very small creature, full-grown specimens being about 1·5 mm. in length. The sexes are separate and of similar size and outward shape. The body is nearly colourless and transparent, with, however, some brownish epidermal pigment in the head and a greenish-brown tinge towards the middle, due to the presence of granules in the wall of the alimentary canal. When mature the ripe spermatozoa, or ova, give an opaque, white appearance to the hinder region of the body.

The worms were found in large numbers in the tank, apparently spending most of their life at the bottom, in the mud chiefly composed of diatoms and other algæ. These plants form their exclusive diet. When undisturbed the Nerilla creeps about a flat surface, moving by means of the ciliated ventral groove which extends along the

[1] I immediately wrote to M. de Beauchamp, who courteously urged me to publish my observations, as his own are still incomplete and unlikely to be finished for some time. With his approval, then, this paper is published, giving for the sake of completeness a full description of my results with very little alteration.

ventral surface of the body. It proceeds evenly along, with passive parapodia, only twisting its head from side to side and using the prostomial and first pair of parapodial cirri as feelers. In this way it progresses at a fair speed.

Occasionally, however, and especially when disturbed, it may rise up from the bottom swimming, or rather darting, swiftly for a short distance with a sudden rapid sinuous motion of the body, as already noticed by de Quatrefages. Alighting on some new spot the worm will then continue its even course propelled by cilia alone. The parapodia are used chiefly when the worm is climbing over a rough surface. When placed in a shallow dish of sea-water Nerilla may often be seen floating near the top close against the surface film; if disturbed it darts away to the bottom.

Nerilla has an aversion to light; it is negatively phototactic. Thanks to this property I was able to devise an easy method of collecting large numbers from the mud in which they live. The method is as follows: A flat dish with about an inch of sea-water is placed near a window, and in it is gently dropped some mud at the end near the light. In a short time a solemn procession of the little worms is seen issuing from the mud and moving towards the darker end of the dish. Here they gather, and can then be easily taken up in a pipette.

They are very hardy; it is easy to keep them alive in ordinary sea-water for several days even in quite a small capsule. In filtered sea-water free from bacteria, but to which have been added some of the algæ on which they feed, they will thrive. I have a large number alive and breeding in Oxford, which were kindly sent to me from Naples by post last July by Mr. K. R. Lewin.

External Morphology.

The body consists of a prostomium, nine trunk segments, and a pygidium (fig. 1). Two pairs of eyes are placed on the dorsal surface of the prostomium, and in front of these three tentacles or prostomial cirri project forwards (figs. 1, 2). The median tentacle is generally raised up slightly above the two lateral tentacles which diverge from it; these are usually carried with their tips quite near the ground. All the tentacles are movable and jointed, and provided with sensory hairs. On either side, just in front of the ventral mouth, is a club-shaped movable palp, projecting from the ventro-lateral surface of the prostomium. Sensory hairs are set on the palps, and their anterior surface is strongly ciliated (figs. 2, 3). Where the prostomium joins the first segment is a deep ciliated groove on each side, it is the sensory nuchal organ commonly found in Archiannelids and in the Polychæta (figs. 1, 2.)

Each of the nine trunk segments bears a pair of parapodia. The segments vary in length, becoming shorter at the hind end of the body; the first is not quite as long as the second, which is the longest of all. No well-marked inter-segmental grooves are visible, but indistinct annuli, five or six in number in most segments, occur all along the trunk.

The parapodia are blunt hollow outgrowths of the body wall, to some extent retractile and elongated dorso-ventrally. Except in the first segment, each is provided with a dorsal and a ventral bundle of chætæ, and except in the last segment with a slender cirrus between them (fig. 4). The parapodium of the first segment is smaller than the succeeding ones. It bears only a dorsal bundle of chætæ, but its cirrus is much longer and more like the prostomial tentacles, both in structure and function, than are those of the other segments (figs. 1, 9). They are generally carried pointing directly outwards or slightly forwards. The chætæ of the first parapodium also differ from those of the other segments, being fewer in number (from 4–6) and pointing almost directly backwards (figs. 1, 2).

The cirri of the next seven segments are indistinctly jointed, and provided with sensory hairs; but they diminish in length and in the number of joints towards the hind end. They are also less movable, being carried stiffly sloping backwards.

The last parapodium has no cirrus, retaining, however, the usual two bundles of chætæ. De Beauchamp states that in his specimens the last segment only bears one bundle of chætæ.

All the chætæ are simple and needle-shaped, with distal ends tapering to a fine point (figs. 1, 4). They are firmly embedded, in bundles of about ten to sixteen, in a cushion of epidermal tissue, which can be moved by appropriate muscles attached to the inner surface of the body-wall (figs. 8, 15). Thus, although the chætæ are arranged in dorsal and ventral bundles, the parapodia are not divided into a noto- and a neuropodium as in most Polychæta. But the parapodia resemble very closely those of Saccocirrus in general character, without, however, being so retractile.

In the presence of chætæ in the parapodia of the first segment Nerilla differs, so far as I am aware, from all known Chætopods. It may be considered as primitive in this respect, since the absence of chætæ on this segment is probably due to a process of cephalisation, which can only be looked upon as secondary.

The anus is dorsal to a triangular pygidial tail process bearing two long jointed anal cirri. These are similar to the other cirri just described, but rather stouter (figs. 1, 5, 20). Rows of glandular cells, secreting a sticky substance, are situated on the ventral surface of the pygidum and its posterior process (fig. 7). This region serves as an adhesive organ whereby the worm can fix itself on to some foreign object.

The mouth is large, with a crescentic lip forming its posterior limit, and a less well-defined bilobed lip in front (fig. 3). Cilia spread over the ventral surface of the prostomium and over the front and lateral walls of the buccal cavity. A ventral ciliated tract extends along the whole length of the body from immediately behind the mouth to the tip of the caudal appendage (figs. 3, 9). It flattens out just behind the mouth and on the pygidium; but along the rest of the trunk forms a definite deep groove easily seen in sections (fig. 36). In the male this ciliated groove is interrupted on the seventh segment by the median genital pore (figs. 10, 20, 24).

An incomplete ring of cilia runs up from below on to the dorsal surface of the prostomium between the lateral tentacles and the eyes (fig. 2). As in Dinophilus, there is a gap between the two halves on the top of the head. Similar but more extensive incomplete rings of cilia are seen behind each parapodium, from the second to the eighth inclusive (fig. 1). These ciliated rings appear to vary considerably in their development; in some specimens they are certainly complete dorsally on the segments behind the second, and they often are continued ventrally so as to join the longitudinal ciliated tract. Behind the ninth pair of parapodia the ring of cilia surrounding the anus is complete (fig. 5). Half-way between each successive pair of parapodia, from the first to the last, is situated on the side of the body a little patch consisting of some five or six rows of ciliated cells on a thickening of the epidermis (figs. 1, 8, 27 *scp.*) Possibly it represents a segmental sense-organ; but I have no positive evidence of its sensory nature. These patches were first described by de Quatrefages as "mamelons ciliés" (**16**), and mistaken by Claparéde (**3**) for the nephridiopores.

The nephridial and genital openings will be described later.

The Epidermis, Nervous System, and Sense-Organs.

A very delicate cuticle covers the whole surface of the worm. Under it lies the epidermis, usually thin, but thickened here and there in special regions. Large gland-cells are found on the prostomium, and also gathered together on the ventral surface of the body, forming bulging masses projecting far into the cœlom at the base of the parapodia (figs. 18, 25 *gl.*) Gland-cells are also present, as already mentioned, on the ventral surface of the pygidium, and extend in diminishing numbers up the ciliated groove (fig. 7). Refringent granules occur dispersed in the epidermis, particularly on the head, where they are especially numerous in the region of the nuchal organ. Here the granules are of a brownish tinge, and lend a colour to the skin.

The nervous system consists of a brain and two longitudinal cords extending on either side of the ventral ciliated groove to the posterior end of the body (figs. 2, 20, 35, 36). The whole system adheres closely to the epidermis, being, in fact, so intimately connected with it that no clear line of demarcation can be made out except on certain parts of the brain. While the nerve-fibres are chiefly grouped on the inner surface, the ganglion cells occupy the outer region. The brain is a bilobed mass lying on the ventral and lateral walls of the prostomium below the origin of the tentacles (fig. 35). From it arise two œsophageal connectives, which pass down on either side to join the ventral cords (fig. 37). No ganglionic swellings or aggregations are to be seen on these cords; but fine transverse fibres connect the two, and nerves pass out to the peripheral parts. Unfortunately the nervous system does not differentiate with methylene blue, so it is scarcely possible to follow it out in detail.

Sensory hairs occur on the palps, tentacles, and cirri; especially near the distal ends of the joints.

Of the four eyes the first pair is the larger, and is directed outwards and forwards (fig. 2). This is determined from the position of the distinct lens lying in the deeply pigmented yellow-brown cup. The hinder, smaller pair point outwards and backwards.

As observed by Miss Pereyaslawzewa, the eyes are very brilliant; against a dark background they shine like the eyes of a cat in the dusk. The nuchal organ is in the form of a deep crescentic groove, with thick edges, and strong cilia on the posterior face of the depression (fig. 2). It communicates by a deep groove with the mouth (fig. 3). It has already been mentioned that lateral ciliated patches occur on each segment, which may possibly act as sense-organs (fig. 1).

The Alimentary Canal.

A straight alimentary canal, ciliated throughout, stretches from mouth to anus (fig. 20). The mouth leads into the buccal cavity, from the floor of which arises the so-called muscular pharynx (fig. 35), a ventral diverticulum. No cilia are present on the lining of this pharynx; its shape is somewhat oval, and its ventral wall very thick and muscular. In fact it closely resembles the similar organ found in other Archiannelids, such as Dinophilus, Protodrilus, and Saccocirrus as already pointed out by de Beauchamp (**2**).

Sections through the pharynx of Nerilla, both transverse and longitudinal (figs. 35, 37), are very like corresponding sections given by Pierantoni in his fine monograph of Protodrilus. In Nerilla, however, there is no thick deposit of cuticular substance such as occurs in Protodrilus, nor are there any teeth as in the Histriobdellids. The pharynx of Nerilla is more like that which I have described in Saccocirrus,[1] though not quite so much developed (**8**).

The narrow œsophagus widens out into the stomach in the second segment. Immediately in front of the stomach lie the salivary glands on each side, consisting of a mass of unicellular glands (figs. 1, 35, 37, *œgl.*). The gland-cells are very granular, and stain very deeply in a quite characteristic manner. Their ducts can be traced for the most part forward to the anterior edge of the fold overhanging the muscular pharynx. Here they open into the buccal cavity,

[1] Both Salensky (**19**) and Pierantoni (**15**) deny the existence of the muscular pharynx which I described in Saccocirrus (**8**). I can only account for these authors' statements on the supposition that they investigated incomplete specimens. Saccocirrus often reaches the laboratory after rough handling, and in a somewhat mutilated condition. The pharynx is probably eversible, and may very possibly be torn off. There can be no possible doubt that it is normally present in Naples specimens; it can be seen in living and in preserved worms, and is, of course, quite easy to make out in sections, both transverse and longitudinal (see figures 1, 19, and 20, on plates 27 and 29 of my paper on Saccocirrus [**8**]).

just as they do in Protodrilus according to Pierantoni (**14**). A few of these cells may sometimes be found scattered on the anterior wall of the œsophagus, and some may open independently into its lumen. Salivary glands quite similar in structure and staining properties have been described by Nelson in Dinophilus conklini (**18**).

The limit between the œsophagus and the stomach is generally marked by a circular fold; the limit between the stomach and intestine is still more definitely shown by a pyloric thickening of the wall surrounding the lumen in the sixth segment (fig. 1). Running along on each side of the stomach wall is a band of gland-cells, very conspicuous in section owing to the great avidity for stains of the granules which fill them (figs. 13, 21). The glandular band begins a little way behind the front end of the stomach, reaches its greatest development about half-way down, and dies away again before the pylorus. The cells which compose it open independently into the cavity of the stomach, passing between the ordinary ciliated epithelial cells. Their swollen bodies, full of granules, bulge outwards on to the surface of the epithelium, giving the wall of the gut the appearance of being formed of more than one layer (fig. 13). Quite similar cells scattered in the wall of the stomach have been described by Nelson in Dinophilus (**18**). Strangely enough, Miss Pereyaslawzewa mistook these gland-cells for developing germ-cells in both sexes (**13**). A ventral groove runs along the intestine, due to a slight folding of the floor, and along it the cilia, at all events at times, work forwards, as is so often the case in Syllids. Immediately in front of the anus there is a quite short rectal region with thick ventral wall; presumably it represents the proctodæum.

The Cœlom and General Mesoblastic Tissues.

There is a clearly defined body-cavity having all the essential characters of a cœlom. The cœlom of the first segment extends into the prostomium: it is closed off by a septum passing behind the pharynx. The septa separating the next three segments are very incomplete in both sexes, so that their cavities communicate freely with each other. In the male complete septa occur between segments 4 and 5, 5 and 6, 6 and 7, and 7 and 8; in the female only the first three of these septa appear to be complete. In sections cœlomic epithelium can be seen to cover the alimentary canal, and, of course, the two faces of the septa. It is less distinct, though still traceable, on the nephridia (figs. 13, 36). On the other hand, it is very difficult to make out on the body-wall, and I am not sure that a distinct epithelium exists here separate from the muscles. The cœlomic cavity extends up the hollow tentacles, palps, and cirri (figs. 4, 35); it reaches the tentacles as a median channel over the brain, which divides into three canals at their base (fig. 35).

A nearly complete ventral mesentery extends along the greater length of the alimentary canal below the longitudinal ventral blood-vessel (figs. 22, 23). The dorsal longitudinal mesentery is much less complete, remaining only here and there as narrow strips.

Very few cœlomic corpuscles are to be seen floating in the cœlomic fluid. A few cells with small granules occur separate or in strings in the first segment. Spreading in all directions through the cœlom is found a peculiar mesenchymatous network, which is of considerable morphological interest, and may possibly take the place of the floating corpuscles more usually found in Annelids. This network has exceedingly delicate branches, and is best studied in the living worm, where it is seen to consist of branching cells forming slender strands, chiefly longitudinal, with the finest threads of protoplasm extending to all the surrounding surfaces. A portion of the network is shown in fig. 8, stretching from the body-wall to the stomach. Similar strands pass up the cavity of the tentacles and cirri, or join the nephridia to the neighbouring parts (fig. 15).

The significance of this mesenchymatous network will be discussed below when treating of the body-cavity in the Archiannelids.

The Vascular System.

There is a simple vascular system, discovered and described by de Beauchamp (**2**). The blood being colourless and the walls of the vessels exceedingly delicate, it is very difficult to follow out the whole course of the system even in sections. As stated by de Beauchamp, there is a distinct peri-intestinal sinus extending over the dorsal and lateral surface of the intestine and hinder part of the stomach; from this sinus springs a median dorsal vessel, which runs forwards above the œsophagus to the head, where it divides into two branches. These pass backwards and downwards on either side of the pharynx,[1] and join to a median ventral vessel running along below the stomach and intestine (figs. 30, 37, etc.). The vascular system is represented diagrammatically in fig. 20. Besides the vessels just mentioned there is in the female a lateral vessel not hitherto observed. It comes off the longitudinal ventral vessel in the sixth segment, and runs over the surface of the ovarian sac, appearing to end in the peri-intestinal sinus (figs. 28, 34). This vessel serves, no doubt, as the indirect source of nourishment for the eggs which develop inside the sac. The walls of the blood-vessels are formed of contractile cells, probably in a single row.

The Muscular System.

The muscles have already been described by Miss Pereyaslawzewa and de Beauchamp (**13**, **2**). The system is but little developed, and consists essentially of two dorsal and two ventral bands of longitudinal muscles running from head to tail. The dorsal are weaker and more flattened than the ventral (fig. 31). A few fibres more median are seen

[1] Salensky (**19**) denies the existence of the similar vessels described by me in Saccocirrus (**8**). There can be no doubt, however, of their presence.

between the large bands above the ventral groove (fig. 36). From the extreme anterior end of the œsophagus muscles extend to the base of the median tentacle over the brain; similar muscle-fibres pass through the brain to the lateral tentacles. The dorsal longitudinal muscles are attached to the ventral wall of the pygidium behind. Some muscles run obliquely through the cœlom from near the nerve-cords to the body-wall, where they are attached chiefly in the neighbourhood of the parapodia (fig. 30). Special muscles are fastened to the pharynx, and others run from the body-wall to the chæta-sacs, whereby these can be to some extent drawn in and out (fig. 8). No distinct layer of muscles can be made out in the wall of the stomach or intestine, nor can circular muscles be seen in the body-wall.

The Nephridia.

Nephridia were first seen in Nerilla by Claparède, who, however, misunderstood their structure (**3**). He believed them to have no internal opening, and to open forwards to the exterior in the centre of the ciliated lateral patch. Miss Pereyaslawzewa denied the existence of nephridia, mistaking them for parasites. De Beauchamp has given a very brief, but correct, account of their disposition and structure (**2**).

There is a marked difference between the sexes in the number and distribution of the nephridia. While in the female there are four pairs of nephridia, in the male there are only three pairs. Those of the male are situated in the second, fifth and ninth segments (fig. 10), those of the female in the second, fifth, sixth and eighth segments (fig. 9). The first and second pairs of nephridia are the same in the two sexes; but the last pair differs not only in position but also to a slight extent in structure. De Beauchamp seems to have missed the nephridia in the ninth segment of the male. All the nephridia are simple, and built on essentially the same plan. The nephridiopore is placed on the ventral surface about halfway between the base of the parapodium and the mid-ventral groove (figs. 9, 10, 15). Inwards from the pore passes the tube coiled in a single twist and forming a swollen body lying at the base of the parapodium. Springing from this body a post-septal canal runs straight to the septum in front, through which it opens into the next segment by the funnel.

Structural details can best be seen in the second nephridium, which is the longest and best developed of the series (fig. 16). The small, but widely open funnel bears on its outer and lower lip a number of extremely long cilia, which work down the canal. A few similar long cilia are attached to the wall of the nephridial canal further down its course. The wall of the post-septal canal is formed of finely granular cells at first, but as it nears the coiled region the wall thickens, and large vacuoles appear in it (figs. 16, 17). These vacuoles soon reach a great size; they are present throughout the coiled region, disappearing again near the nephridiopore. Each is filled with a clear liquid, in the centre of which is suspended a large, very highly refringent granule, constantly agitated with the Brownian movement. Both the granule and the liquid are probably of an excretory nature, and are, I believe, discharged into the lumen of the nephridium. Very conspicuous in the living worm, these granules were noticed long ago by Claparède (**3**). No cell outlines are visible in the nephridium; in sections the vacuoles are seen to be much more numerous than the rare nuclei (fig. 36). The lumen is almost certainly intra-cellular.

The first nephridium is rather smaller than the second, but scarcely differs from it in structure. On the other hand the third in the female generally appears of looser texture, with less regularly disposed vacuoles, and a wider lumen sometimes irregularly distended at intervals. It is a little smaller than the second, but larger then the first. By far the smallest nephridium is the last, in the ninth segment of the male and in the eighth segment of the female. The lumen of this nephridium is less coiled and is often greatly distended (fig. 15).

The Genital Organs of the Male.

No correct account has yet been given of the very interesting genital organs of the male Nerilla. It has already been mentioned that ordinary nephridia do not occur in segments 6, 7, and 8. In these three segments are developed three pairs of sperm-ducts, all converging to a common pore at the posterior limit of the seventh segment (figs. 10, 19). We shall discuss below whether these ducts are modified nephridia as suggested by de Beauchamp (**2**). Miss Pereyaslawzewa saw the median pore, but thought the sperm-cells were developed in the wall of the gut, and apparently mistook epidermal glands for parts of the testes (**13**).

The six sperm-ducts are of similar structure, but of varying lengths, the first pair being by far the longest. Each consists of a slender tube of uniform thickness and a cœlomic funnel. The inner wall of the tube is clothed with closely set, fine, short cilia working towards the external pore (fig. 12). Piercing the septum, the duct widens out into a funnel which opens into the segment in front. The funnel consists of a few symmetrically disposed cells, bearing numerous fine cilia on the surface of the septum (figs. 12, 22, 24). The six spermiducal funnels lie, then, on the septa between segments 5 and 6, 6 and 7, 7 and 8, opening into the cœlom of segments 5, 6, and 7 (figs. 10, 19).

The six sperm-ducts converge to a common chamber lying in the middle line at a point where the ciliated groove is interrupted (figs. 6, 24).

This median chamber, or genital atrium, also ciliated, is blind in front, but opens behind by a pore, the edges of which are drawn out on each side to form two small processes. I believe these to serve for copulation, but have not observed them in action.

The copulatory processes are formed as epidermal outgrowths, and are not ciliated. Backwards from the genital pore the ventral ciliated groove resumes its course. Special epidermal glands are related to the male genital aperture. They form a four-cornered area on the ventral surface of segments 7 and 8 (fig. 6), and are doubtless to be interpreted as specialisations of the ordinary glands found at the base of the parapodia in other segments. Composed of a right and left set of unicellular glands, their long ducts converge towards and open into the genital atrium. The swollen bodies of these gland-cells are for the most part aggregated in four masses at the four corners of the glandular area, and situated at the base of the seventh and eighth pairs of parapodia (figs. 6, 19). Here they bulge far into the cœlomic cavity (figs. 23, 25). The granular contents of these cells are peculiar, and differ from those of glands in other parts in that they acquire a brownish tinge and become highly refractive in balsam.

A pair of testes is situated in segment 5 (fig. 19). Each testis has a narrow anterior end running forward parallel to, and on the inner side of, the neck of the nephridium, until it reaches the base of the septum separating the fifth from the sixth segment (fig. 21). Here it merges with the cœlomic epithelium. Behind the testicular cord enlarges, passes up the side of the gut to join the testis of the other side in a large median dorsal mass loosely compacted and somewhat irregular in shape (figs. 19, 22). The youngest cells are, of course, found at the front end of the testis near the septum. They multiply and grow backwards, the ripest cells being in the dorsal mass, chiefly formed of sperm-morulæ, which become detached and float off. Finally, fully developed spermatozoa abound in segment 5 in mature specimens. This fifth segment is shut off in front and behind by complete septa, preventing any spermatozoa from straying into neighbouring cavities. As the production of spermatozoa increases the anterior septum bulges forward as a median sac into the fourth segment, and the posterior septum bulges backward into segments 6 and 7 (fig. 19). Ripe spermatozoa are carried down the first pair of sperm-ducts to the genital pore. We should expect to find testes in segments 6 and 7, corresponding to the second and third pairs of sperm-ducts, but it is a remarkable fact that I have never found true spermatozoa belonging to these segments. However, there are organs which must be considered as homologous with testes, although not producing true spermatozoa. Occupying the same position as the testes in segment 5 are found, in segments 6 and 7, two cords of cells starting from the cœlomic epithelium on the septa between the segments 5 and 6, and 6 and 7 (figs. 19, 26). They enlarge behind into masses, soon breaking up into spherical cells, which float off in the cœlomic fluid. Segments 6 and 7 always contain a large number of these rounded cells, very conspicuous in the living worm owing to their refringent contents, especially in large and ripe specimens. But the cells in segment 6 differ from the cells in segment 7, those in the first of these segments being more spherical and containing numerous minute refringent granules (fig. 19A), while those in the seventh are less regular in shape and hold only a few large oval granules (fig. 19B). We have, then, a very remarkable state of things in the adult male Nerilla—namely, three consecutive segments provided with testis-like organs producing different kinds of floating cells; in the first true spermatozoa, in the second cells with small granules, and in the third cells with large granules (diagrammatically shown in figs. 19 and 20). The cavity of each of these segments is shut off by complete septa, and from each two ducts lead to the common pore; but whether the granular cells are really carried out to the exterior I have not yet ascertained for certain. It may be that they contribute to the formation of the seminal fluid. It might be thought that the males I have examined were exhausted, that the sixth and seventh segments produced spermatozoa first, and that, after these had been expelled, the granular cells took their place. But there is no evidence to support this view. The granular cells are found in small as well as in large individuals.

The Genital Organs of the Female.

It has already been mentioned that nephridia occur in segments 2, 5, 6, and 7 of the female Nerilla, but neither in segment 9, nor in segment 7. In the living worm two slender oviducts can be detected occupying the place of the nephridia in segment 7. They are delicate tubes, lined with fine closely set cilia, passing backwards from the septum between segments 6 and 7, to open separately on the ventral surface near the base of the parapodium, at a point corresponding to the nephridiopores in other segments (fig. 11). Towards the external pore, which is elongated and oblique, converge a number of granular unicellular gland-cells (figs. 11, 18, 34). The internal opening of the oviduct is in the form of a small funnel piercing the septum, and spreading out on its anterior face (fig. 11). Sections show the funnel as a small patch of ciliated epithelium with a central opening leading into the duct (fig. 32). The oviducts seem extraordinarily small as compared with the ripe ova; in sections the diameter is actually less than that of the nucleus of the ovum and even than that of its nucleolus. But it is possible that the duct enlarges just before the eggs are laid, as in so many worms; moreover the egg is very soft, and no doubt capable of squeezing through a small aperture. A similar disproportion is often found in the Oligochæta.

The ovaries are situated in segment 6 (figs. 18, 30). Each pear-shaped ovary is attached at its anterior narrow end to the septum in front not far from the middle line. Sometimes the two almost fuse below the gut (fig. 36). Towards the free posterior end of the ovary the cells increase in size, forming a compact chain of growing ova with granular cell-bodies and large vesicular nuclei (fig. 31). A right and a left ovarian sac enclose the ovaries (figs. 1, 29–34). A blood-vessel runs over the outer surface of the ovarian sac, the inner lining of which is composed of large granular cells forming a very conspicuous deeply staining epithelium (fig. 14). These cells appear to build up yolky material for the nourishment of the growing ova. When an ovum reaches a certain size it drops off into the cavity of the ovisac, becomes surrounded with a thick porous membrane, and filled with a dense mass of yolk-granules (figs. 29–34). The ova grow to a very large size, become opaque and white, and subsequently make their way through the wall of the sac into the cœlom of the neighbouring segments (figs. 1, 27, 32). Such ripe ova escape chiefly behind, but occasionally in front of the ovarian sacs. When in front they may bulge into segment 5, pushing septum 5, 6, forwards. When behind, they may form a chain of egg-cells pushing the septa back until they reach the last segment of the body. As many as eighteen ripe ova may be found in one female.

The disposition of the ovaries, ovisacs and ripe ova is always asymmetrical (figs. 1, 18)—a peculiar feature for an annelid. While the ovisac of the left side grows forwards, that of the right side grows backwards. The asymmetry of the ovisacs is accompanied, if not caused by, a twisting forwards of the free end of the left ovary, so that the largest ova are pushed towards the head, while the free end of the right ovary grows more naturally backwards towards the anus. Thus the large ova are packed along the long axis of the body, and the intestine is forced to adopt a sinuous course between them. It is, I believe, for the sake of economising space, and more easily packing the ripe ova, which have to be retained for a considerable period in the cœlom, that this asymmetrical structure has been adopted.

On the inner lower surface of each ovisac is developed a little pocket, always filled with a darkly staining mass (figs. 18, 28, 31). The pocket lies a little farther forward on the right than on the left side. Probably these are the vesicles described by Miss Pereyaslawzewa as being filled with spermatozoa and connected with ducts. They are, however, quite independent of the oviducts, though situated near them. That fertilisation in Nerilla is internal seems very probable, considering that the male is provided with what are doubtless copulatory appendages (fig. 6), and that internal fertilisation has been shown to occur in Saccocirrus, Dinophilus, and Histriobdella. But it is one of the points I have not yet been able to determine for certain. Never have I seen spermatozoa in a living female; but in one series of sections of a female which has shed its large ova, numerous spermatozoa are present in the ovisacs.

An account of the maturation of the germ-cells and of the embryology is reserved for a future paper. The eggs are laid in groups, each being enclosed in a transparent shell. Development is direct; there being no free-swimming larva the young are hatched as little worms.

The Morphology of the Genital Ducts.

The absence of nephridia in the genital segments might lead one to conclude that nephridia have been directly converted into genital ducts in these segments; but this is almost certainly not the case. Much more probable is it that the ducts are nephromixia, or mere cœlomostomes (**6**, **7**). In Protodrilus, Pierantoni has described large-funnelled organs in the sexually mature worm, which have all the appearance of nephromixia (**14**). These ducts closely resemble the nephromixia of the Syllids, formed at maturity by the grafting on to the nephridial funnel of a large funnel derived from the cœlomic epithelium (**7**). Somewhat similar tubes are found in Saccocirrus (**8**), which, at all events in the male, are probably of the same compound nature. More difficult to interpret is the case of Polygordius. Here the genital products escape by breaking through the body-wall, and the cœlomostomes have consequently degenerated. The nephridium of the larva is closed and provided with solenocytes (**7**, **9**), and the nephridium of the adult opens by a true nephrostome (see my fig. 46, Pl. 42, **7**). If cœlomostomes are developed at all, it can only be at the time of maturity, and to a small extent. Funnels, apparently of cœlomic origin, have indeed been described by Fraipont (**5**) and Hempelmann (**12**). On the other hand it is very doubtful whether the nephridia take any share whatever in the formation of the genital ducts in Histriobdella and Dinophilus. In these two genera the nephridia are still closed in the adult. That their special genital ducts are not merely modified nephridia I have already maintained when, in 1894, treating of the homology of nephridia and genital ducts in general (**6**). I then came to the conclusion, which still seems to me the best, that the ducts of Dinophilus (and also of Histriobdella) are formed chiefly by the cœlomostome to which the nephridium may possibly contribute a small portion. In all these Archiannelida, then, the genital ducts appear to be formed by the cœlomostomes, with which the nephridia may perhaps have combined to form nephromixia, such as are known to occur in the Polychæta. The same interpretation obviously applies to Nerilla. That the genital ducts in both sexes of Nerilla are of the nature of cœlomostomes can hardly be doubted, but again here, as in the other cases discussed above, a final conclusion cannot be reached without the evidence of embryology. The absence of nephridia in the genital segments, and the position of the genital pores in the female, may be taken to support the view that the nephridia have been included in the ducts.

Coming now to the resemblances of the genital organs of Nerilla and other Archiannelids, we may notice first of all that in Dinophilus (**24**), Histriobdella (**23**), and Protodrilus (**14**), the ova are very similar in structure and behaviour. In all these worms the ripe ova undergo the preliminary stages of maturation in the cœlom of the female parent, where they usually have been precociously fertilised. The sperm-ducts of Dinophilus resemble those of the Histriobdellids (**10, 11**); in both cases there is a median opening provided with a penis. In Saccocirrus the openings and the copulatory organs are paired and numerous (**8**). Nerilla resembles the former genera in the possession of a median opening, and in the structure of the ducts, but the penis is represented only by paired processes. In the possession of three pairs of sperm-ducts the male Nerilla may be considered as more primitive than the female, and as more primitive than Dinophilus and Histriobdella. For in Archiannelids, as in Oligochætes, specialisation seems to have led to a restriction of the gonads to fewer and fewer segments. In Polygordius and Protodrilus a large number of segments are fertile, in Saccocirrus only the middle region produces gonads, in the male Nerilla three segments, and in the female one; finally, in Dinophilus and Histriobdella a single pair of gonads is present in both sexes. Accompanying this reduction is a corresponding diminution of the number of ducts.

The Body-Cavity in the Archiannelids.

Nerilla throws a new light on the structure of the aberrant Dinophilids and Histriobdellids. It has often been held (Harmer [**10**], Schimkewitsch [**20**], Shearer [**22**]) that the general body-cavity of Dinophilus is not of cœlomic, but of blastocœlic or of hæmocœlic origin; that the cœlom is represented by the cavity of the ovarian and testicular sacs alone. Several years ago (**6**) I adopted this view myself, and Shearer has recently applied it to Histriobdella (**23**), but it now seems to me much more probable that these two genera are as specialised in the development of the cœlom as they are in many other characters. Already Fœttinger has described a cœlomic cavity, and a cœlomic epithelium, extending throughout the anterior segments of Histriobdella (**4**), and Salensky (**19**) has drawn attention to the secondary invasion of the cœlom by a network of "cœlenchym" in Saccocirrus and Protodrilus. To put the matter shortly, the course of specialisation seems to have been as follows: In Dinophilus and Histriobdella the gonads have become restricted to one segment, the cavity of which is shut off by complete septa, and so forms a sac ("ovary," or "testis"). The septa in other regions have broken down, and the cœlom has become invaded by a secondary ingrowth of mesoblastic tissue. Already in Nerilla, as shown above, the anterior septa have almost completely disappeared, and a delicate network of mesenchymatous fibres extends in all directions through the cœlom.

It would be only necessary to carry this process a little further to bring about the state of things found in Dinophilus. That this interpretation is correct would seem to be proved by the discovery of a rudimentary separate blood-space in Histriobdella (Shearer [**23**]), and of a comparatively well-developed vascular system in Dinophilus by de Beauchamp (**1**). Moreover, it is quite in accord with what we know of the nervous system, with its distinctly segmented structure and metameric ganglia, and also of the development of the mesoblast, segmented in early stages (Schimkewitsch [**20**]), We may conclude, then, that all the Archiannelids originally had a normal segmented cœlom.

The Affinities of Nerilla.

At first sight Nerilla looks like a very small Syllid. For a considerable time I was deceived by this resemblance, and it was placed among the Syllids by its early describers. If Nerilla were a worm of larger size its extraordinary likeness to a Syllid would very possibly be taken for an instance of mimicry, but no such significance seems attributable to the resemblance in this case. The deception is due not only to general outward shape, but also to internal structure. The eyes, the palps, the parapodial and pygidial cirri, and more especially the three prostomial tentacles, all recall the Syllid. Yet these cirri and tentacles differ from the corresponding processes in Syllids in being hollow, and the parapodial cirri differ also fundamentally from those of Polychætes in being placed between the bundles of chætæ, and not above or below them. The nephridia are not unlike, and the œsophageal glands strangely simulate the paired diverticula so often found in the Syllidea.

Yet there can be little doubt that the resemblance is not due to affinity, and that Nerilla belongs, not to the true Polychæta, but to the Archiannelida. Nerilla is interesting because it is the most Polychæte-like of all the Archiannelids, and because it occupies a central position among the widely differing genera of that group. The affinities of Nerilla are not with one genus in particular, but with several. It thus binds the Archiannelida together, while at the same time to some extent bridging over the gap between them and the Polychæta.

Comparison of Nerilla with other Archiannelids.

In common with Dinophilus and Protodrilus, it possesses a ventral ciliated tract, which forms a distinct longitudinal groove as in Protodrilus. These three genera also are provided with very similar ciliated rings. Simple parapodia are found in Saccocirrus similar to those of Nerilla in structure, but differing in the presence of only one bundle of chætæ instead of two; a point in which the latter approaches the true Polychætes. Possibly the tentacles of Polygordius, Protodrilus and Saccocirrus are homologous with the lateral tentacles of Nerilla, in spite of structural differences; but it is undoubtedly the Histriobdellids which come nearest to it in the possession of shorter but similar processes on the head and trunk segments. The nervous system, closely connected with the epidermis, bears a marked resemblance to that of Protodrilus. The alimentary canal of Nerilla is very like that of Dinophilus; as in all Archiannelids, with the single exception of Polygordius,[1] there is a muscular ventral pharynx. The pharynx is unarmed, as in Dinophilus and Saccocirrus. The nephridia are more like those of Polygordius, Protodrilus, or Saccocirrus in general structure; in distribution and specialisation in the two sexes they resemble those of Dinophilus and Histriobdella. Certain specialisations in the glands and ducts of the genital organs and the presence of a median male pore seem also to point to affinity with these two genera.

In a work on Saccocirrus published some years ago (**8**), I pointed out that the absence of chætæ in some Archiannelids cannot be considered as a primitive character, since Sacco-

[1] See footnote on p. 404.

cirrus must be classified with Protodrilus, and Saccocirrus has parapodia with chætæ on most of the segments of the trunk. This conclusion has been remarkably confirmed by the happy discovery made by Moore (**17**), of a genus allied to Polygordius, Chætogordius, bearing chætæ on some segments. Salensky and Pierantoni (**19, 14**) also agree that Protodrilus is closely allied to Saccocirrus. Taken as a whole the Archiannelida form a degenerating series which can only be read one way. But very possibly the group includes three such series starting from a common Chætopod ancestor, Chætogordius and Polygordius forming one, Saccocirrus and Protodrilus another, and Nerilla, Dinophilus, and Histriobdella a third.

Summary.

Nerilla is an Archiannelid, with a prostomium, a pygidium, and nine trunk segments bearing parapodia. There are three cirri on the prostomium, two on the pygidium, and one on each parapodium except the last. The cirri are slender, hollow, jointed processes, with sensory hairs. A ventral ciliated groove extends from mouth to anus; ciliated rings occur on the prostomium and on the trunk segments, and there is a ciliated patch on each side of each segment. The first parapodium bears one bundle, and the other parapodia two bundles of simple chætæ. The cirrus is placed between the bundles. The central nervous system, throughout closely connected with the epidermis, consists of a brain and two ventral nerve-cords without ganglionic swellings. The prostomium carries four eyes and two nuchal organs. The alimentary canal consists of an œsophagus, stomach, intestine and short rectum, all ciliated, and a ventral muscular pharynx. Unicellular glands open into the buccal cavity, and gland-cells are greatly developed on either side of the stomach. The cœlom is well developed; but some of the septa are very incomplete. Cœlomic corpuscles are very rare; a delicate network of cœlenchyme extends throughout the body-cavity. A simple vascular system is present. The nephridia have

open funnels, a slightly coiled lumen, and vacuoles containing one refringent concretion. Nephridia are present in segments 2, 5 and 9 of the male, and in segments 2, 5, 6 and 8 of the female. The male has three genital segments, 5, 6, and 7. In the first only do the testes produce spermatozoa; in the second and third the testes appear to be degenerate and to produce granular cells, with small granules in segment 6, and large granules in segment 7. Three pairs of similar ducts correspond to these three segments. The six sperm-ducts open into a common median ventral genital atrium, which leads to a median pore with a small copulatory process on each side. Special epidermal gland-cells open into the genital atrium. Two ovaries are present in the sixth segment of the female. Each ovary becomes enclosed in an ovisac, lined by nutritive epithelium; the ovisacs are asymmetrically developed. Full-grown ova escape from the sacs into the cœlom of the sixth segment, and are retained for a long time in the parent, passing forwards or more often backwards along each side of the gut. Here they undergo the preliminary stages of maturation. It is possible, but not yet certain, that fertilisation is internal. A pocket, containing deeply staining cells, is found on the inner side of each ovisac. Two oviducts are present, leading from the sixth segment to paired genital pores on the seventh segment. Epidermal glands converge towards the pores. The eggs are laid in transparent capsules, development is direct, and the young emerge as small worms with only one median tentacle and about five segments.

Nerilla combines primitive with specialised characters. The parapodia, chætæ, cœlom, and number of the gonads and their ducts have become progressively reduced in the Archiannelids. They are probably modified forms descended from Chætopod ancestors. The genital ducts appear to be either cœlomostomes, or cœlomostomes combined with nephridia (nephronixia). Nerilla preserves many Chætopod characters, but has affinities with several genera, more especially perhaps with Histriobdella and Dinophilus.

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EXPLANATION OF PLATES 38–41,

Illustrating Mr. Edwin S. Goodrich's paper on "Nerilla an Archiannelid."

Reference Letters.

a. Anus. *ac.* Anal cirrus. *ae.* Anterior eye. *blv.* Blood-vessel. *bn.* Branching network of cœlenchyme. *br.* Brain. *bw.* Body-wall. *c.*$^{1-9}$. Cœlom of segments 1–9. *cep.* Cœlomic epithelium. *cgl.* Clear gland-cells. *ch.* Chætæ. *chs.* Chæta-sacs. *ci.* Cilia. *con.* Concretion. *cop.* Copulatory process. *cr.* Cirrus. *cri.* Ciliated ridge. *crg.* Ciliated ring. *cvg.* Ciliated ventral groove. *dchs.* Dorsal chæta-sac. *dlm.* Dorsal longitudinal muscles. *dv.* Dorsal blood-vessel. *ep.* Epidermis. *gat.* Genital atrium. *gl.* Gland-cells. *go.* Genital opening. *gr.* Groove. *grc.* Granular cells. *lc.* Cells with large granules. *lo.* Lateral nuchal organ. *lt.* Lateral tentacle. *m.* Mouth. *mt.* Median tentacle. *nv.* Nerve cord. *neph.* Nephridium. *nf.* Nephrostome. *np.* Nephridiopore. *oblm.* Oblique muscles. *œs.* Œsophagus. *œgl.* Œsophageal glands. *om.* Oblique muscles. *ov.* Ovum. *ovd.* Oviduct. *ovdf.* Oviducal funnel. *ovdgl.* Oviducal gland. *ovs.* Ovisac. *ovy.* Ovary. *p.* Pocket of ovisac. *pe.* Posterior edge. *ph.* Pharynx. *plp.* Palp. *pp.*$^{1-9}$. Parapodia of segments 1–9. *r.* Rectum. *rt.* Modified testis. *s*^{1}. Segment with spermatozoa (first genital). *s*^{2}. Segment with granular-cells (second genital). *s*^{3}. Segment with cells loaded with large granules (third genital). *scp.* Segmental ciliated patch. *sp.* Developing spermatozoa. *spd.*$^{1-3}$. Three pairs of sperm-ducts. *spf.* Spermiducal funnel. *spt.* Septum. *ss.* Septal sac. *st.* Stomach. *td.* Dorsal-lobe of testis. *vbw.* Ventral body-wall. *vchs.* Ventral chæta-sac. *vlm.* Ventral longitudinal muscles. *vnc.* Vacuole in nephridial cell. *vv.* Ventral blood-vessel.

Nerilla antennata, O. Schmidt.

PLATE 38.

Fig. 1.—Dorsal view of a female; enlarged.

Fig. 2.—Dorsal view of the head; enlarged.

Fig. 3.—Ventral view of the same.

Fig. 4.—Semi-diagrammatic view from behind of a parapodium, showing chætæ and cirrus.

Fig. 5.—Dorsal view of the posterior end of the body, ♀; enlarged.

Fig. 6.—Ventral view of a ♂, showing the genital pore and atrium enlarged.

Fig. 7.—Ventral view of the pygidium, ♀; enlarged.

Fig. 8.—Ventral view of the side of the third and fourth segments, showing the network of "cœlenchym" in the cœlom; enlarged.

PLATE 39.

Fig. 9.—Ventral view of a ♀, to show the disposition of the nephridia and genital ducts; enlarged.

Fig. 10.—Similar view of a ♂.

Fig. 11.—Enlarged view of a left oviduct; from the living.

Fig. 12.—Enlarged view of the funnel of a left sperm-duct; from the living.

Fig. 13.—Portion of a transverse section of the wall of the stomach; enlarged.

Fig. 14.—Surface view of the wall of the ovisac; enlarged; from the living.

Fig. 15.—Ventral view of the last nephridium of a ♂; enlarged; from the living.

Fig. 16.—Enlarged view of the second nephridium; from the living. For the most part in optical section.

Fig. 17.—Surface view of a portion of the same.

PLATE 40.

Fig. 18.—Diagram of a dorsal view of the posterior segments of a ♀, showing the glands, nephridia, and genital organs.

Fig. 19.—Similar view of a ♂.

Fig. 19 A.—Enlarged view of the granular cells from the sixth segment of ♂.

Fig. 19 B.—Enlarged view of the granular cells of the seventh segment of a ♂.

Fig. 20.—Diagram of a longitudinal section of a ♂.

Fig. 21.—Transverse section of a ♂ through the fifth segment. Z. 3 mm. oil imm., oc. 3. cam.

Fig. 22.—Transverse section of the same through the fifth segment; cutting the funnel of the sperm-duct.

Fig. 23.—Transverse section of the same through the seventh segment.

Fig. 24.—Transverse section of the same through the genital atrium.

Fig. 25.—Transverse section of the same through eighth segment.

Fig. 26.—Transverse section of the same through the degenerate testis of the seventh segment.

PLATE 41.

Fig. 27.—Transverse section of a ♀ through the fifth segment. Z. 3 mm. apoch., oc. 4 cam.

Fig. 28.—Transverse section of the same through the sixth segment.

Fig. 29.—Transverse section of the same through the sixth segment, further back.

Fig. 30.—Transverse section of the same through the sixth segment, further back.

Fig. 31.—Transverse section of the same through the sixth parapodium.

Fig. 32.—Transverse section of the same through the funnels of the oviducts.

Fig. 33.—Transverse section of the same through the oviducts in the seventh segment.

Fig. 34.—Transverse section of the same through the seventh segment, further back.

Fig. 35.—Longitudinal section through the head region, nearly median. Z. D., oc. 4, cam.

Fig. 36.—Ventral portion of transverse section passing through the front end of the ovaries. Cam., Z. 3 mm., oc. 8.

Fig. 37.—Transverse section passing through the muscular pharynx. Cam., Z. D., oc. 4.